
CONTRIBUTIONS TO PALÆONTOLOGY

I

NEW MIDDLE PLIOCENE RODENT AND LAGOMORPH
FAUNAS FROM OREGON AND CALIFORNIA

By ROBERT W. WILSON

With three plates

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NEW MIDDLE PLIOCENE RODENT AND LAGOMORPH FAUNAS FROM OREGON AND CALIFORNIA

INTRODUCTION

The purpose of this paper is the description of two rodent faunas in the collections of the California Institute of Technology. Although coming from widely separated areas, these assemblages are of approximately the same age. The first fauna to be discussed is that from Pliocene strata near Rome, Malheur County, Oregon. It exhibits some diversity of type although the associated larger mammals are known by very fragmentary remains. The second rodent fauna comes from the Kern River deposits, San Joaquin Valley, California. The Kern River rodents and lagomorphs, and the larger mammals found with them, share with other Tertiary assemblages of the San Joaquin Valley the important task of determining the time relationships between the nonmarine deposits in which they are found and the standard marine sections of the Pacific Coast.

The illustrations for this paper are from photographs by the late H. Wm. Menke, and have been carefully retouched and arranged into plates by John L. Ridgway.

ROME FAUNA

The Rome fauna occurs in lake beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, five miles southwest of Rome, Malheur County, Oregon. Locally, in the fossiliferous area, the section consists of light green to white tuffaceous sandstones, pebble beds, and mudstones. Most of the fossils were obtained from a narrow band of sediments situated near the base of the section as exposed along the eastern side of Dry Creek, a small tributary of Crooked Creek. Except for an isolated cheek-tooth of *Castor*?, the entire rodent fauna was obtained from this limited stratigraphic zone.

The following rodent and lagomorph types have been recorded from the Rome fauna:

Rodentia

Mylagaulus? cf. *monodon* Cope

Dipoides stirtoni Wilson

Castor? sp.

Goniodontomys disjunctus n. gen. and sp.

Lagomorpha

Hypolagus vetus (Kellogg)

Hypolagus sp.

Associated with the above assemblage are rather fragmentary mammalian remains representing a diverse fauna. These remains have not been studied in detail, but the following forms have been recognized in the fauna:

<i>Scapanus(?)</i> sp.	Felid large sp.
<i>Plihippus</i> near <i>spectans</i> (Cope)	Felid small sp. (possibly <i>Machærodont</i>)
<i>Teleoceras fossiger?</i> (Cope)	Camelid large sp.
<i>Prosthennops</i> sp.	Camelid small sp.
<i>Sphenophalos nevadanus</i> Merriam	Cervid sp.
<i>Lutra</i> sp.	Mastodont sp.
<i>Plionictis</i> near <i>ogygia</i> (Matthew)	Turtle, fish, reptile, and bird remains
<i>Lutravus</i> cf. <i>halli</i> Furlong	
? <i>Ælurodon</i> sp.	
Canid (in <i>Ælurodon-Osteoborus</i> group) probably n. gen.	

Work on the Rome fauna has not been intensive enough to determine the exact time relations of the assemblage. However, a middle Pliocene age or a stage of evolution comparable to that represented by the Rattlesnake-Thousand Creek faunas seems certain. More particularly, the Rome rodent fauna suggests by the presence of *Castor?* and of a vole that it is at least as advanced as the Thousand Creek fauna.

The presence, in the Rome assemblage, of a mole, beavers, an otter, and fish remains points to a rather moist environment with bodies of water in the immediate vicinity. The limited collecting area, the lithology of the sediments, and the large number of specimens of *Dipoides* suggest that the deposits are lacustrine in origin.

SYSTEMATIC DESCRIPTION OF FAUNA

RODENTIA

Mylagaulidæ

The Mylagaulidæ present many problems which need to be solved before a satisfactory understanding of the group is reached. Not only are the various species in considerable confusion, but even the genera are in an uncertain state of definition. The relation of horned to hornless types has not been determined, nor have the limits of individual and age variation been fixed.

It has been suggested that the presence or absence of horns is a sex character. However, as Matthew has pointed out, no other known rodent possesses a like amount of sex distinction, although, as he states further, this argument is partly vitiated by the fact that no other rodent possesses horns. Such a variation, in a burrowing form in which the horns were presumably used as digging implements, would

place the female at a decided disadvantage. Moreover, the California Institute of Technology collections embrace a number of Miocene and Pliocene mylagaulids complete enough to demonstrate the presence of horns if such structures were actually present. However, no horns were noted, and it is extremely unlikely that all these skulls and similar specimens found elsewhere represent females. Judging from published descriptions, horned types are everywhere relatively rare.

It can be shown rather satisfactorily that the tooth-pattern undergoes considerable change during the life of the individual. The variation in the skull is not known, nor is there a suitable answer to the question of individual variation in premolar pattern. In certain species the individual variation of teeth representing approximately the same stage of wear is not great. However, if the conclusion implied by this statement is applied widely, an extremely large number of species in proportion to the number of known specimens would have to be recorded. Moreover, some of the mylagaulid material in the Institute collections points to considerable individual variation in specimens from the same zone and locality.

By means of relatively unworn teeth it is possible to demonstrate in the upper premolar the derivation of the lakes from the original basins in the unworn teeth and, moreover, the origin of certain dental areas from particular cusps, exactly as this has been done in the cheek-teeth of such forms as *Equus*. The lower premolar appears susceptible to a similar treatment, although greater difficulty is encountered in tracing the derivation of the adult pattern than in the upper premolar. Use of this method of study leads to a clearer appreciation of the differences or similarities in two distinct species than can be obtained by citing the number of lakes present and their arrangement in varying numbers of rows. It is felt that this method of study combined with sectioning of individual teeth might eventually lead to an understanding of the characters exhibited by isolated grinding teeth. Such work would have to be based primarily on a thorough study of species which are known by a large number of specimens and in which teeth in all stages of wear are present.

Doubtless a greater number of species and perhaps genera are in existence than have been described. It is conceivable that such eminently burrowing types might have a rather limited geographic range and that consequently a number of distinct species might be present in each faunal stage. However, with our present understanding of the group, the establishment of more types is decidedly not a desirable procedure.

Pliocene mylagaulids are known only by fragmentary material. A possible exception is *Epigaulus hatcheri*, the type of which consists

of a fairly complete skull and skeleton. Gidley referred the beds (Republican River) from which the type was obtained to the upper Miocene. The type locality is near Long Island, Kansas. Stirton¹ has recently referred a fauna, termed by him the Long Island fauna, to the middle Pliocene. *Mylogaulus monodon* and *M. sesquipedalis* also have been recorded from Pliocene beds. The type localities of these two species are in the Republican River beds, and hence the exact age of the specimens is not known, although they are usually referred to the lower Pliocene. A referred specimen of *M. monodon* apparently comes from the same beds as *E. hatcheri*. Matthew has suggested that *M. monodon* may have to be referred to *Epigaulus* and states that *M. monodon* and *E. hatcheri* are probably identical.² However, Matthew in describing the type of *M. monodon* states that P₄ has no cement outside the external enamel ring. The type of *E. hatcheri*, as described by Gidley, possesses premolars in which an investment of cement forms a functional part of the teeth. This discrepancy can be removed only by assuming: (1) that cement was present originally on the type of *M. monodon* and has dropped away; (2) that the type was incorrectly described (not probable); or (3) that the presence or absence of cement is not a distinctive character. Perhaps the explanation given under (1) is the most likely. *M. sesquipedalis* is distinguished from *M. monodon* by its smaller size, fewer, less elongate lakes, and more irregular arrangement of lakes.

Mylogaulus? cf. monodon Cope

Pliocene mylogaulids from the Great Basin have been known hitherto only by two isolated grinders. A P₄ has been recorded by Miss Kellogg³ from Thousand Creek, Nevada, and E. Raymond Hall has described a lower premolar from the Fish Lake Valley beds of Nevada.⁴ In comparison, mylogaulid material from Rome is relatively abundant. The most perfectly preserved specimen is an almost complete lower jaw, C.I.T. No. 72 (Plate 1, figs. 8, 8a, 8b). The extreme tip of the coronoid is missing, as is the posterior portion of the angle, but the dentition is complete including all three molars. A second ramus, No. 1951, which was also obtained is more fragmentary than No. 72. The dentition in this specimen lacks M₁. Isolated premolars, Nos. 1952-1958 (Plate 1, figs. 1-7), both upper and lower, and various fragmentary limb elements are present also in the Rome collection. The two rami represent young individuals in which practically none of the enamel inflections has become isolated, thus making comparisons with other specimens difficult. All the remains have been considered as representing a single species, although this is a doubtful procedure with reference to one or two specimens.

The Rome species is characterized by premolar teeth which become elongate in a fore-and-aft direction with wear. The enamel lakes are

¹ R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, no. 8, 284, table 3, 1934.

² W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, art. 2, 75, 1924.

³ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 429, fig. 10, 1910.

⁴ E. R. Hall, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, no. 12, 307-308, figs. 18-19, 1930.

numerous, elongate, and tend to arrange themselves in rows. The teeth possess an external investment of cement which in some specimens at least is a functional part of the tooth. The ramus is very heavy and deep, thick transversely below the premolar. P_4 possesses from six to usually nine lakes. The single specimen exhibiting six lakes, No. 1954 (Plate 1, fig. 2), is relatively unworn and indicates that an increase in the number of lakes takes place with further wear. The lower premolars possess a minimum of eight lakes in a well-worn tooth and a maximum of nine, although this figure might be increased to ten. The teeth are larger than those of *Mylogaulus laevis* but smaller than in the type of *Epigaulus hatcheri*. A mylagaulid humerus is distinctly smaller than the comparable element in *E. hatcheri*.

The Rome species does not agree exactly with any described species, but may be closest to *M. monodon*. Compared with the type of *M. monodon*, the Rome species possesses a larger ramus, which is deeper and more distinctly bulged by the premolar. P_4 is narrower transversely and possesses a larger number of lakes. The latter show a somewhat different arrangement. A P_4 referred by Cope to *M. monodon* agrees in size and shape with the Oregon type but the occlusal pattern appears to be distinct. If both the type and referred specimen of *M. monodon* are actually conspecific, the Rome specimens are rather close to them. However, cement forms a functional part of the wearing surface of the premolar, a character in which they differ from *M. monodon* as described by Matthew.

Epigaulus hatcheri Gidley,¹ although with larger $P_4/4$, resembles the type from Rome in the presence of an external coat of cement on the cheek-teeth. The ramus of the Rome species apparently possesses slightly different proportions, but is thick and deep below P_4 , a character seen in *E. hatcheri*. The tooth-row is slightly shorter in the Oregon form, and $P_4/4$ differ somewhat in pattern in the two species. If *E. hatcheri* and *M. monodon* are conspecific, the type from Rome would be close to that species. However, the upper premolars of the Oregon type show a close agreement with those of a species of mylagaulid from Bartlett Mountain, Oregon (Pliocene). A very well-preserved skull of the latter is without bony horn-cores, a character in which it differs distinctly from *Epigaulus*.

Mylogaulus species from Fish Lake Valley, Nevada, is represented by a single isolated P_4 . This species is smaller than the Rome type with somewhat different occlusal pattern. Unfortunately, the dimensions of the figures given by Hall do not agree very well with his measurements. In any case the species is probably distinct from that found at Rome.

The only other Pliocene mylagaulid material on record from the Great Basin is an unworn P_4 from the Thousand Creek beds, described by Miss Kellogg. This specimen was referred by her to *M. monodon*. Although Miss Kellogg compared this tooth directly with figures of the type of *M. laevis* Matthew in the belief that the latter was still referred to *M. monodon* Cope, the Thousand Creek form is probably closer to Cope's species than to *M. laevis*. However, in the case of the Virgin Valley specimen, referred by Miss Kellogg to *M. monodon*, the figure shows a tooth more closely resembling *M. cf. laevis* from Skull Spring than *M. monodon*. U.C. No. 12580, a P_4 referred to *M. pristinus*, may also represent the Skull Spring species. Virgin Valley mylagaulids in the California Institute collection indicate the presence of a species distinct from the Skull Spring type. Whether this second

¹ J. W. Gidley, Proc. U. S. Nat. Mus., vol. 32, no. 1554, 627-636, pls. 58-65, 1907.

species is referable to *M. pristinus* was not determined. An isolated P4 in the Institute collection from Thousand Creek appears to be distinct from the Rome species.

The fragmentary limb material from Rome is too incomplete to add anything to our knowledge of the skeletal structure of the Mylagaulidæ.

It is quite possible that *Mylagaulus?* cf. *monodon* from Rome represents an undescribed species of rodent. In view of our very incomplete knowledge of the Mylagaulidæ nothing would be gained by establishing a new species.

Measurements (in millimeters) of Mylagaulus? cf. monodon Cope

	No. 72	No. 1951
P4-M3, alveolar length	19.1	17.8
Length of diastema, I-P4	10.6	...
Depth of ramus beneath P4	18.9	...
Depth of ramus beneath diastema	12.6	...
Thickness (transverse) of ramus beneath P4	11.8	...
	Maximum	Minimum
Several isolated P4's:		
Greatest antero-posterior diameter	12.0	11.0
Greatest transverse diameter	6.4	5.6
Several isolated P4's:		
Greatest antero-posterior diameter	13.3	10.4
Greatest transverse diameter	6.0	5.2

Castoridæ

Dipoides stirtoni Wilson

Remains of this species of aberrant beaver are very common in the Rome fauna. A detailed account of the fossil material has already been published.¹

Castor? sp.

The true beaver is represented by a single isolated M2?. This specimen, No. 1961 (Plate 1, figs. 9, 9a), represents an individual comparable in size to the existing *Castor canadensis*. The base of the tooth is somewhat damaged, but practically the full height of the cheek-tooth seems to be preserved. Three internal and one external lateral grooves are present, as is normal for *Castor*. The external groove extends to the base of the portion preserved, while the three internal inflections extend somewhat less than half the distance to the base of the tooth. In a measure, the extent of the internal grooves is a function of the amount of wear the tooth has undergone, but undoubtedly the grooves are much less persistent than in Recent species. The posterior groove (metastrid) is slightly longer than the other two (mesostrid and parastrid), which are equal in length. The occlusal pattern is that of a normal *Castor* except for the presence of an enamel lake in the anterior enamel loop. Such a lake is present in the first molar of a ramus of the Asiatic *C. andersonni*, as figured by Schlosser.² However, in this species M1 and M2 are shorter transversely than is the Rome molar, although M2 has the same antero-posterior diameter, and M1 only a slightly greater measurement. *C. andersonni*, together with the Asiatic species *zdanskyi* and *broilii*, has been placed by Young in a new genus *Sinocastor*. The

¹ R. W. Wilson, Carnegie Inst. Wash. Pub. No. 453, pt. 3, 1934.

² M. Schlosser, Palæ. Sin., ser. C, vol. 1, fasc. 1, pl. 2, fig. 43, 1924.

present author has not observed the above-mentioned lake in any other specimens of *Castor*.

There may be some doubt as to the association of the Rome *Castor*? with the rest of the rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity, raise this question. However, not only does the association in the field of *Castor*? with *Pliohippus* teeth obviate this possibility to a large extent, but the characters exhibited by the specimen itself point in the same direction.

True beavers from North America are extremely rare in beds older than the upper Pliocene. Two teeth from the upper Snake Creek (P4 and P4) and the present one are all that have been so far recorded. The geologic range of *Castor* is not accurately determined, but the genus or closely allied types are known from the early Pliocene of Europe and Asia.

Measurements (in millimeters) of Castor? sp.*

M2?, antero-posterior diameter.....	8.2
M2?, transverse diameter.....	7.1

* Measured at occlusal surface.

Microtinæ?

Goniodontomys disjunctus n. gen. and sp.

Geological Age and Locality—Middle Pliocene beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, five miles southwest of Rome, Malheur County, Oregon.

Genotype—No. 1959, C.I.T. Coll. Vert. Pale., an incomplete left ramus bearing M1–M2 (Plate 2, figs. 2, 2a, 2b).

Referred Specimen—No. 1960, C.I.T. Coll. Vert. Pale., a small fragment of ramus with left M2 in place.

GENERIC AND SPECIFIC CHARACTERS

Mandibular incisor passing from lingual to buccal side of tooth-row, and probably extending well up into the ascending ramus. Cheek-teeth hypsodont, prismatic, and flat-crowned, rooted and without cement. Re-entrant angles of cheek-teeth generally opposed. Re-entrant angles from opposite sides normally in contact. Enamel not differentiated into thick and thin tracts. M1 with posterior loop, three triangles, and complex anterior loop. Second external salient angle of M1 opposite third internal salient angle.¹ Ramus heavy and apparently shortened. Length of tooth-row approximately as in *Mimomys primus*.

DESCRIPTION

Inferior Dentition—The mandibular incisor crosses from lingual to buccal side of the tooth-row under (?) M3, and probably extends well up into the ascending ramus. The first molar (Plate 2, fig. 2) is composed of a pos-

¹The system used by M. A. C. Hinton for enumeration of the re-entrant and salient angles has been adopted in this paper. See Hinton, *Monograph of the Voles and Lemmings (Microtinæ) Living and Extinct*, vol. 1, 22, 1926. To quote from Hinton: "In describing the teeth it is customary to enumerate the salient angles and re-entrant folds from before backwards in upper molars, and from behind forwards in lower molars, the first salient angles on each side being formed by the transverse loop."

terior loop, three triangles, the anterior two opposed to form a somewhat tetragonal loop of enamel, and a complex anterior loop. The anterior loop is complicated by a pronounced inflection on the internal side, a similar but less pronounced inflection buccally, and an antero-median inflection in front. A very shallow fold of enamel is also present on the buccal side and just anterior to the main external fold mentioned above. The posterior triangle communicates broadly with the posterior loop, but the commissures connecting the median pair of triangles with the anterior and posterior portions of the tooth are narrow. M $\overline{2}$ is a less complex tooth which may be characterized as possessing three loops of enamel connected by narrow commissures. The median loop is apparently analogous to the two posterior alternating triangles in normal voles. A second, less worn specimen of *Goniodontomys*, No. 1960, possesses slightly more triangular salient angles, and in addition some slight angulation of the anterior loop suggestive of the two more or less alternating triangles which replace this loop in the normal vole dentition. M $\overline{2}$ is distinctly shorter than M $\overline{1}$.

Ramus.—The ramus (Plate 2, figs. 2a, 2b) is rather deep and is apparently shortened. The juncture of ascending and alveolar portions of the ramus occurs opposite the posterior root of M $\overline{1}$ as in voles, rather than opposite the posterior root of M $\overline{2}$ as in *Neotoma*. The ridge for attachment of the masseter muscle terminates anteriorly about opposite the posterior surface of the anterior root of M $\overline{1}$. The masseter medialis scar is slightly less developed than the preserved portion of the masseter lateralis scar. The mental foramen is situated close to the superior surface of the ramus, and almost directly beneath the anterior tip of M $\overline{1}$. A second small foramen is found just above the tip of the ridge for the attachment of the masseter muscle. The area for symphyseal attachment extends back well under the posterior portion of M $\overline{1}$. In this character our genus resembles *Microtus* and differs from *Neotoma*. In the latter genus the symphyseal area is much more limited posteriorly.

RELATIONSHIPS

Although the systematic position of *Goniodontomys* is not entirely clear, it has been assigned to the Microtinæ. The genus is known by such fragmentary material that it is difficult to eliminate from consideration some other groups of rodents with hypsodont teeth. *Goniodontomys* is widely separated from most microtines by the more or less complete opposition of the usually alternating prisms of the cheek-teeth. The second molar has an occlusal pattern somewhat like that exhibited by some species of *Hyperacrius* and *Eothenomys*. The first molar, however, is quite unlike the usual microtine M $\overline{1}$, especially in the nearly opposite second external and third internal salient angles. In voles of more normal type, when the triangles are opposite one another, the second external triangle or salient angle is opposed by the second internal triangle. An approach to the pattern of M $\overline{1}$ in the Oregon genus is made in a specimen of *Prometheomys schaposchnikowi*,¹ figured by Hinton, but the resemblance is remote. Moreover, the anterior termination of M $\overline{2}$ in *Goniodontomys* is not angular, as is usually the case in Microtinæ. No. 1960, the dentition of which is somewhat less worn than the type, suggests this angular termination, and some Recent voles possess second molars with a more or less rounded appearance.

¹ M. A. C. Hinton, *Monograph of the Voles and Lemmings*, vol. 1. Brit. Mus. Nat. Hist., 86, fig. 55, 1926.

Relationship to the microtines is suggested in *Goniodontomys* by the thin enamel of the cheek-teeth, the triangular shape of the salient angles, the relatively large number of elements comprising M1, and various characters in the ramus. If the intermediate-external triangle of M2 and the internal triangles of M1 of *Goniodontomys* were shifted anteriorly, an occlusal pattern would result quite close to that in many microtines.

If *Goniodontomys* is to be assigned to the Microtinæ, the genus is a vole and not a lemming. Enough of the mandibular incisor is preserved in the type specimen to demonstrate this conclusion.

Reference of *Goniodontomys* to some group of rodents other than the microtines seems less likely than the present assignment. A number of rodent families possess members with hypsodont teeth, but most of them are quite removed structurally as well as geographically from the Oregon genus. *Neotoma* and its relatives suggest a relationship with *Goniodontomys* in certain features of the dentition. However, the dentition of *Neotoma* has relatively thick enamel borders, the salient angles are less triangular, the ramus is slimmer, and the ascending ramus rises from the horizontal ramus farther back than in *Goniodontomys*. Moreover, not only does *Goniodontomys* possess a more complicated M1, but it is hardly likely that any *Neotoma*-like form from the middle Pliocene would be so high-crowned as is the case in the former genus. The second lower molar of *Neotoma* is strikingly like that of *Goniodontomys* in the general aspect of the pattern. On the other hand, in our genus the second external salient angle and the third internal salient of M1 form a loop directed forward and inward. The corresponding loop in *Neotoma* is more transverse or, if oblique, is directed slightly forward and outward. A fossil species of *Oxymycterus*, *imperus* Ameghino from the Pampean of South America, resembles *Goniodontomys* more closely in pattern of M1 than does *Neotoma*. However, M2 is quite different and the resemblance is probably superficial.¹

The cape-rats possess extremely hypsodont teeth with occlusal patterns quite similar to that of microtines. However, the group has never been recorded from North America and its dental pattern resembles that of *Goniodontomys* less than does that of some voles. Moreover, early Pliocene forms are known from Asia, and these are no closer to our genus in occlusal pattern than are existing types. The early Pliocene Asiatic specimens show a pronounced tendency to isolate the re-entrant folds of enamel as lakes. In this respect *Goniodontomys* is closer to normal microtines, in which such a condition is limited to extreme wear.

Other groups of rodents with hypsodont teeth have decidedly less resemblance to *Goniodontomys* than do those mentioned above. Such forms as *Sigmodon*, the jerboas, and the Gerbillinæ differ in one or more major characters.

If *Goniodontomys* is a vole, it is the oldest so far recorded. Unfortunately, it is not very close to existing forms, and apparently represents an aberrant type. It is surprising that the Microtinæ are not more common in the Tertiary, as the subfamily must have had a considerable geologic range. *Poamys* Matthew from the lower Snake Creek was regarded by Matthew as possibly a structural ancestor of the Microtinæ. The validity of this hypothesis cannot be determined on available evidence. However, the presence of *Goniodontomys* and *Poamys* in beds older than the upper Pliocene sug-

¹ F. Ameghino, Contr. al Conocimiento de los Mam. Fos. de la Republ. Argent., Actos Acad. Nac. de Ciencias Republ. Argent. en Cordoba, Atlas, pl. 4, fig. 3b, 1889.

gests the possible presence of other microtine-like forms in the late Miocene and early Pliocene.

Since *Goniodontomys* is an aberrant type, it does not furnish much evidence as to the evolution of the Microtinæ. The opposition of the triangles in this genus does not necessarily demonstrate that this is the primitive microtine condition, although the perfect alternation of prisms seen in many voles is probably a specialized and advanced character.

Measurements (in millimeters) of Goniodontomys disjunctus n. gen. and sp.

C.I.T. No. 1959 (genotype). Middle Pliocene, Rome, Oregon

Length of crown, M1-M2.....	5.5
M1, antero-posterior diameter.....	3.0
M1, transverse diameter.....	1.5+
M2, antero-posterior diameter.....	2.2
M2, transverse diameter.....	1.5
Depth of ramus beneath M1.....	6.3

LAGOMORPHA

Leporidae

Hypolagus vetus (Kellogg)

Several fragmentary lower jaws and a number of isolated teeth, both uppers and lowers, appear to be referable to *Hypolagus vetus* (Kellogg).¹ The Rome specimens are of approximately the same size as topotype material of *H. vetus* from Thousand Creek. Characters exhibited by P3 agree with those of the latter material except that this tooth in the Rome form may be slightly broader on the average, with flatter or more gently rounded anterior face, which serves to widen this portion of the tooth. Some topotype specimens exhibit these characters, but the average specimen is probably somewhat different. The lower molariform teeth, as seen in No. 1962 (Plate 2, figs. 3, 3a), fragmentary left ramus with P3-M1, and No. 1963, fragmentary left ramus with P3-M1, C.I.T. Coll. Vert. Pale. from Rome, may be slightly larger than comparable material from Thousand Creek.

A single isolated P2 is present in our collections. If this tooth is referable to the same species as the rami, it differs from the Thousand Creek *H. vetus* in a lengthening of the tooth transversely. However, the specimen shows a deep antero-internal fold and a shallower antero-external fold as in *H. vetus*. The upper molariform teeth do not seem to show such heavy external ribs as in the Nevadan species.

C. L. Gazin has referred a large species of *Hypolagus* from Hagerman to *H. near vetus*.² In shape of P3 and in size of some specimens at least, the Rome material is close to that from Hagerman. If the Rome fauna is actually advanced over that from Thousand Creek, as is perhaps suggested by the presence of *Castor*?, the Thousand Creek, Rome, and Hagerman specimens may form a progressive series. However, it is doubtful if the Rome fauna as a whole is more advanced than that from Thousand Creek.

Compared with other known species of *Hypolagus*, the Rome specimens are readily distinguished by their large size as well as by characters in the dentition.

¹ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 436-437, fig. 20, 1910; L. R. Dice, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, no. 12, 181-182, figs. 4-5, 1917.

² C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, no. 2976, 112-114, fig. 1, 1934.

A large series of topotype material of *H. vetus* was available for comparison. It should be noted that this material shows decided variation in the characters of P3 as well as some variation in most of the other characters that have been used to establish species of *Hypolagus*. The Rome material is too scanty to permit one to say that the specimens average differently from those from Thousand Creek, although study of the collection suggests this to a certain extent. However, since certain specimens from Thousand Creek are closely comparable to individuals from the Oregon locality, the specific designation is justified.

Measurements (in millimeters) of Hypolagus vetus (Kellogg)

	No. 1962	No. 1963
P3-MI, occlusal length.....	9.1	9.3
Depth of ramus below MI, measured on inside.....	12.7	..

Hypolagus sp.

A left ramus of *Hypolagus* with P4-M3, No. 1964 (Plate 2, figs. 1, 1a), appears to represent a species distinct from *H. vetus*. This specimen is characterized by a much lighter dentition than is present in *H. vetus*, although the ramus is as deep and apparently as robust. The lower molari-form teeth have convex postero-internal ribs, most noticeably developed in P4 and MI. This surface is flattened in typical *H. vetus*. *H. vetus* from Rome may be intermediate in this respect. Several additional specimens representing individuals smaller than those of *H. vetus* in the collection have also been referred tentatively to this type. One isolated P3 is present which is smaller than the comparable tooth of *H. vetus*. Aside from difference in size, the tooth is close to the *vetus* type.

Comparison of the Rome species with small species of *Hypolagus* is handicapped by lack of suitable material. However, the robust jaw of the Rome form would seem to distinguish this species from others in which the dentition is similar in size.

It should be stated that sufficient material is not available to obviate the possibility that this second species of *Hypolagus* represents merely a young or immature stage of *H. vetus*. Comparisons, as stated above, are based mostly on a single ramus. A second jaw apparently possesses a larger dentition, but this is still distinctly smaller than that in *H. vetus* from Rome. Until more material becomes available it seems desirable to recognize two types from the Rome locality.

Measurements (in millimeters) of Hypolagus sp.

	No. 1964
P4-M3, occlusal length.....	8.4
Depth of ramus below MI, measured on inside.....	12.9

KERN RIVER FAUNA

The Kern River deposits are located about nine miles northeast of Bakersfield, in Kern County, California. A middle Pliocene rodent and lagomorph fauna obtained from these beds consists of the following forms:

Rodentia

Citellus? sp.

Peromyscus pliocenicus n. sp.

Lagomorpha

Hypolagus near *limnetus* Gazin

Hypolagus small sp.

SYSTEMATIC DESCRIPTION OF FAUNA

RODENTIA

Sciuridæ

Citellus? sp.

Sciurid remains from the Kern River beds are limited to a right ramus with P4-M2 and an alveolus for M3, No. 1965 (Plate 3, figs. 1, 1a); a second right ramus without dentition; and fragments of an upper and a lower incisor which may be referable also to this family. Specimen No. 1965 is the basis for the doubtful generic determination given above.

The dentition of No. 1965 is extremely worn and part of the first molar is missing. As a consequence, comparisons are difficult to make. No. 1965 is relatively small, agreeing in size with Recent specimens of *Callospermophilus lateralis certus*. The molars do not show the pronounced fore-and-aft compression and the high trigonids characteristic of typical *Citellus*, and the specimen certainly does not represent the genus in the restricted sense. P4 is rather triangular in outline and the anterior two cusps were probably closely appressed in their originally unworn condition. The mandibular incisor is relatively broad and lacks pronounced furrows. Thus, No. 1965 appears to represent the genus *Citellus* in a broad way, and to be related to such genera or subgenera as *Callospermophilus* and *Otospermophilus*, which occupy a position intermediate between typical *Citellus* and typical *Sciurus*.

No. 1965 seems to be more closely related to *Otospermophilus gidleyi* (Rattlesnake), *Citellus* sp. (Thousand Creek), and *Citellus?* sp. (Smiths Valley) than to any other Pliocene sciurids. It is about the size of these species and moreover agrees in general character of the dentition, at least in so far as may be observed in the well-worn dentition of the Kern River specimen.

Otospermophilus gidleyi Merriam, Stock, and Moody¹ from the Rattlesnake formation of eastern Oregon approximates the Kern River species in length of tooth-row, but the ramus of the former is deeper. The talonid rim in M2 of No. 1965 may be more angulate than in the Oregon species. Degree of angulation in No. 1965 is difficult to determine because of breaking away of the inner margins of the molars in the specimen. *Citellus?* sp.² from Smiths Valley, central Nevada, also approaches No. 1965 in size, although the tooth-row in the Smiths Valley species may be slightly longer. M2 of the former is slightly larger than the comparable tooth in the latter and may be somewhat more compressed antero-posteriorly. In addition, the mandibular incisor of the Nevadan species is heavier and perhaps slightly more compressed, although degree of compression is difficult to determine accurately with the present material. *Citellus* sp.³ from the Thousand Creek beds of northern Nevada is too inadequately known to permit comparisons. No. 1965 agrees with the Thousand Creek specimen in size. Other Pliocene Sciuridæ appear to be clearly distinguishable from the Kern River species.

For purposes of comparison it may be stated that the alveolar length, P4-M3, in No. 1965 is 8.4 millimeters.

¹ J. C. Merriam, C. Stock, and C. L. Moody, Carnegie Inst. Wash. Pub. No. 347, pt. 3, 68-69, fig. 23, 1925.

² R. W. Wilson, Carnegie Inst. Wash. Pub. No. 473, pt. 2, 19-20, pl. 1, fig. 5, 1936.

³ L. Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, no. 29, 427-428, fig. 8, 1910.

Cricetidae

Peromyscus pliogenicus n. sp.

Type—Fragmentary right ramus with M1-M2, No. 1966, C.I.T. Coll. Vert. Pale. (Plate 3, figs. 2, 2a).

Paratypes—Fragmentary left ramus with M1-M2 and alveolus for M3, No. 1967 (Plate 3, fig. 4); fragment of right maxillary with M1 and incomplete M2, No. 1968 (Plate 3, fig. 3); C.I.T. Coll. Vert. Pale.

Geological Age and Locality—Middle Pliocene Kern River beds, Kern County, California. C.I.T. Locality No. 49.

SPECIFIC CHARACTERS

Cheek-teeth hypsodont, but crowns show tendency to wear to flat surfaces; without accessory folds although intermediate tubercles may be present or absent. M1 with divided antero-median cusp; tip of antero-internal re-entrant angle becomes isolated with wear leaving a broad, shallow re-entrant. M3 relatively unreduced. Pit or foramen in maxillary bone lateral to anterior root of M1. Size large, slightly exceeding any known fossil species, but approximating that of *Peromyscus nesodytes*.¹

DISCUSSION

Peromyscus pliogenicus is distinguished from all other fossil species of the genus, except *P. antiquus* and *P. nesodytes*, by its large size. Even these two species are somewhat smaller, in length of tooth-row, than the Kern River type.

Compared with *P. antiquus* Kellogg² from the Thousand Creek beds of northern Nevada, *P. pliogenicus* is not only larger but is distinguished by the following selected differences: (1) antero-median cusp of M1 divided, resulting in an external cusp rather than a narrow sloping ridge as in the Nevadan species; (2) M1 relatively longer; (3) antero-posterior ridge of M2 may be slightly less developed; and (4) intermediate tubercles are variably developed, whereas they are entirely absent in *P. antiquus*. Relatively large intermediate tubercles are present in the type of *P. pliogenicus* (Plate 3, figs. 2, 2a), but are absent in the paratype No. 1967. Rudimentary intermediate tubercles are also present in the upper cheek-teeth as demonstrated in the paratype specimen, No. 1968.

Peromyscus nesodytes Wilson,³ from the Santa Rosa Island Pleistocene, approaches *P. pliogenicus* more closely in size than does *P. antiquus*. The Kern River species differs from the island form in the following characters: (1) more hypsodont; (2) internal cusps of cheek-teeth perhaps narrower; (3) intermediate tubercles variably developed, whereas in *P. nesodytes* they appear to be absent. (4) M1, although of approximately the same antero-posterior diameter, is perhaps less triangular in outline; the tip of the antero-internal re-entrant angle shows a tendency to become isolated, the remainder becoming very shallow and open in contrast to the more permanent V-shaped notch in *P. nesodytes*. In the relatively unworn M1, the antero-external

¹It is possible that the character of size is more applicable to the cheek-teeth of *P. pliogenicus* than to the individual as a whole. However, the present fragmentary material does not suggest necessarily that this individual possessed relatively large cheek-teeth.

²L. Kellogg, *op. cit.*, 432-433, fig. 16, 1910.

³R. W. Wilson, *Jour. Mamm.*, vol. 17, 408-410, 1 fig., 1936.

re-entrant angle is very deep, extending almost to the anterior margin of the tooth. With wear the tip of this re-entrant also becomes isolated. In *P. nesodytes* this re-entrant angle apparently never was so deep, although wear may have obliterated any enamel islet resulting from isolation. (5) Judging from the alveolus, M3 is less reduced.

Comparative measurements (in millimeters)

	<i>Peromyscus pliogenicus</i>		<i>P. antiquus</i> U.C. No. 12571 (type) Thousand Creek	<i>P. nesodytes</i> C.I.T. No. 1780 (type) Santa Rosa Island Pleistocene
	C.I.T. No. 1966 (type) Kern River beds	C.I.T. No. 1967 (paratype) Kern River beds		
M1-M3, alveolar length.....		6.1	5.2	5.8
M1-M2, alveolar length.....		4.3
M1-M2, occlusal length.....	4.4	4.4	3.9
M1, antero-posterior diameter.....	2.2	2.3	2.0	2.5
M1, transverse diameter.....	1.4	1.5	1.5	1.6
M2, antero-posterior diameter.....	2.0	2.0	1.8	1.9
M2, transverse diameter.....	1.6	1.6	1.6	1.6
M3, antero-posterior diameter.....	1.6	1.5
M3, transverse diameter.....	1.2	1.3

Peromyscus pliogenicus

C.I.T. No. 1968 (paratype). Kern River beds

M1, antero-posterior diameter.....	2.3
M1, transverse diameter.....	1.5?

Other known fossil forms either are much smaller than *P. pliogenicus* or are closely related to living representatives of the genus.

The Kern River species is clearly separable from Recent species of the genus. It is sharply marked off by its large size from all except members of the subgenera *Megadontomys*, *Peromyscus*, and *Haplomylomys*. Some members of the subgenus *Megadontomys* apparently exceed *P. pliogenicus* in size. However, in the former, supplementary enamel loops and tubercles are highly developed, whereas in our species the accessory tubercles between the primary cusps are apparently not always present, and, most important, no accessory loops or folds of enamel enter into the cheek-tooth pattern of either the superior or the inferior dentition. *Megadontomys* is an inhabitant of southern Mexico and Central America.

Many of the southern species of the subgenus *Peromyscus* are characterized by relatively large size. These species are all smaller than the Californian type and, moreover, possess upper cheek-teeth with supplementary tubercles at the buccal margin which wear to form accessory enamel folds in the cheek-teeth. These supplementary folds may be small but are apparently always present. No. 1968, a maxillary fragment of *P. pliogenicus*,

exhibits rudimentary tubercles. However, these cuspules do not enter into the cheek-tooth pattern.

Members of the subgenus *Haplomylomys* possess cheek-teeth without supplementary tubercles or with such tubercles in a rudimentary state of development. The largest species of the subgenus, *P. californicus*, is distinctly smaller than *P. pliocenicus*. Moreover, the accessory tubercles in the dentition of No. 1966 exceed those of any specimen of *Haplomylomys*.

It is not to be assumed, on the basis of the brief and by no means complete comparisons given above, that *P. pliocenicus* bears a close relationship to any Recent subgenus. As a matter of fact, it is highly improbable that any of the modern subgenera were differentiated as early as the middle Pliocene. Limited comparisons with Recent subgenera are given merely as the simplest means of eliminating from consideration the large number of Recent species. However, it is worth noting that large species were common in the middle Pliocene of the United States, whereas now, except for *P. californicus*, the large peromyscine forms are all southern in distribution. This fact may indicate a general southward movement of many of the Pliocene forms with, of course, considerable evolutionary change with the passing of geologic time.

LAGOMORPHA

Leporidae

Hypolagus near *limnetus* Gazin

Leporid remains are rather abundant in the Kern River collection. These remains include fragmentary rami and maxillæ as well as isolated teeth and skeletal parts. Two species appear to be present, the larger of which is near *Hypolagus limnetus* of the Hagerman fauna.¹ The more complete material representing this form includes No. 1969 (Plate 3, fig. 5), a specimen with the palatal portion of the maxillæ preserved with P3-M2 present on both sides; a left maxillary with P2-M2, No. 1970 (Plate 3, fig. 6); a right ramus with P3-M3, No. 1972 (Plate 2, fig. 5); a left ramus with P3-M2, No. 1973 (Plate 2, fig. 4); and a second left ramus with P4-M2, No. 1974. Although the Kern River form is from an older stage, it agrees with *H. limnetus* in approximate size and in the shape of P3, as well as in depth of re-entrant folds in this tooth. P3 is rather broad with the antero-internal border rounded (Plate 2, fig. 4). The antero-external fold is relatively deep, a point of resemblance to the Hagerman type. The character of the plications on the median re-entrant fold of the upper molariform teeth is apparently similar to that in *H. limnetus*. The fold may be slightly less deep and complex on the average, but there seems to be variation in this regard in the Kern River form.

Hypolagus furlongi Gazin² from Grand View is closely related to *H. limnetus*. However, the Kern River form is apparently distinguished by a less triangular P3 with deeper antero-external fold. Moreover, in P2 of *H. furlongi* the antero-internal fold is deep and crenulated. P2 in the Californian material is more like that of *H. limnetus* and is not crenulated.

Other species of *Hypolagus* do not appear to be closely related to the Kern River type. *H. vetus*, although from an approximately equivalent

¹ C. L. Gazin, Proc. U. S. Nat. Mus., vol. 83, no. 2976, 114-117, figs. 2-3, 1934.

² *Ibid.*, 118-119, fig. 4, 1934.

horizon, is larger and possesses a P3 in which the antero-external fold is shallower and the outline of the tooth somewhat narrower anteriorly.

Hypolagus edensis Frick¹ from the middle (?) Pliocene Eden beds is smaller than *H. near limnetus*; the inner borders of the lower molariform teeth are rounded, not angulate as in the Kern River form; and the antero-external fold in P3 is more anterior in position.

Hypolagus? apachensis Gazin² compared with *H. near limnetus* is from an older stage. It is a smaller form with the median fold of the upper molariform teeth less complexly plicated. In addition, P3 is relatively longer and the antero-external fold in that tooth is shallow.

Lastly, *H. browni* (Hay)³ appears to be more advanced in character of the postero-external fold of P3 than is the Kern River species. However, the antero-external fold is relatively less deep than in *H. near limnetus*. This species is smaller and from a distinctly later stage (early Pleistocene?).

The Kern River material agrees more nearly with *H. limnetus* from Hagerman than with any other species of the genus. However, it comes from an earlier stage and may represent a distinct species. Since seven or eight species of *Hypolagus*, representing a wide variety of types, are already known, nothing is gained by separating the Kern River species as a distinct type.

Measurements (in millimeters) of Hypolagus near limnetus Gazin

	No. 1971	No. 1970	No. 1969
P2-M3, alveolar length.....	13.1
P2-M2, occlusal length.....	9.3+
P2-M2, alveolar length.....	11.9
P3-M2, occlusal length.....	8.7—	8.4
Greatest width across antero-ventral prominence of zygomatic arches	30.5
Least antero-posterior length of bony palate.....	5.5

	No. 1972	No. 1973	No. 1974
P3-M3, alveolar length.....	13.5	14.1 (a)
P3-M2, occlusal length.....	10.8—
Depth of ramus beneath M1, measured on outside.....	10.6	10.4

(a) Approximate.

¹ C. Frick, Univ. Calif. Pub., Bull. Dept. Geol., vol. 12, no. 5, 348, figs. 52-53, 1921.

² C. L. Gazin, Carnegie Inst. Wash. Pub. No. 404, 67-69, pl. 3, figs. 1-4, 1930.

³ O. P. Hay, Proc. U. S. Nat. Mus., vol. 59, no. 2391, 630-631, 1921; L. R. Dice, Papers Mich. Acad. Sci., Arts, and Letters, vol. 16, 379-382, figs. 8-11, 1932.

Hypolagus small sp.

Several of the *Hypolagus* specimens from the Kern River beds appear to represent a second, smaller species of the genus. The species is represented by No. 1975, a fragment of left ramus with P $\overline{3}$ -M $\overline{1}$, and several isolated teeth. In contrast to the larger Kern River species, P $\overline{3}$ in this type is somewhat elongate and triangular. Only three third lower premolars in the collection appear referable to the species of *Hypolagus* under discussion. All these teeth are somewhat different, including one, No. 1976, with a postero-internal groove on the side of the tooth in evidence as a slight fold on the occlusal surface of the tooth. The antero-external fold in P $\overline{3}$ is fairly deep but shows a tendency to be quite wide. In one specimen, No. 1975, the anterior limb of the fold is parallel to the axis of the tooth. The lower molariform teeth, as compared with those of *H. near limnetus*, may be relatively a little longer antero-posteriorly, but the limited remains available make this character doubtful. The upper molariform teeth, represented by isolated teeth, may possess median re-entrant folds which are less complexly plicated than in the larger species. This statement is also doubtful in view of uncertainty as to the position of the teeth in the maxillary, and since individual variation is seen in this character when large series of teeth are available for comparison. Moreover, if these teeth are viewed from below they appear to be more complexly folded.

Remains of this species are not complete enough to warrant a specific designation. As a matter of fact, the specimens may represent young individuals, and difference in tooth-pattern between this form and *H. near limnetus* from the same locality may be due to age. Comparisons with known small species of *Hypolagus* were made, but because of the limited material available, proved inadequate to reveal any real relationships.

Measurements (in millimeters) of Hypolagus small sp.

	No. 1975
P $\overline{3}$ -P $\overline{4}$, antero-posterior length.....	5.2

PLATE 1

Myiagaulus? cf. monodon Cope

- FIGS. 1, 4, 5—Isolated right P₄'s; Nos. 1955, 1952 (reversed), and 1953; $\times 2\frac{1}{4}$.
 FIG. 2—Isolated left P₄ (reversed); No. 1954; $\times 2\frac{1}{4}$.
 FIG. 3—Isolated left P₄ (reversed); No. 1956; $\times 2\frac{1}{4}$.
 FIG. 6—Isolated right P₄; No. 1958; $\times 2\frac{1}{4}$.
 FIG. 7—Isolated P₄; No. 1957; $\times 2\frac{1}{4}$.
 FIGS. 8, 8a, 8b—Left ramus with P₄—M₃ inclusive; No. 72. Fig. 8, occlusal view, $\times 2\frac{1}{4}$;
 fig. 8a, intero-lateral view, $\times \frac{1}{4}$; fig. 8b, extero-lateral view, $\times \frac{1}{4}$.

Castor? sp.

- FIGS. 9, 9a—Isolated left M₂?; No. 1961; $\times 2\frac{1}{4}$. Fig. 9, occlusal view (reversed); fig. 9a,
 intero-lateral view.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale. Middle Pliocene, Rome, Oregon.



1



2



3



4



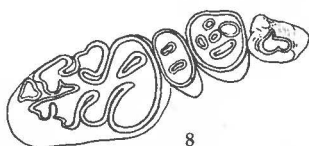
5



6



7



8



9



8^a



8^b



9^a

PLATE 2

Hypolagus sp.

FIGS. 1, 1a—Incomplete left ramus with P4-M3; No. 1964. Fig. 1, occlusal view, $\times 2\frac{1}{4}$; fig. 1a, lateral view, $\times 1\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Goniodontomys disjunctus n. gen. and sp.

FIGS. 2, 2a, 2b—Fragmentary left ramus with M1-M2, genotype specimen; No. 1959. Fig. 2, occlusal view, $\times 9$; fig. 2a, intero-lateral view, $\times 4\frac{1}{2}$; fig. 2b, extero-lateral view, $\times 4\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Hypolagus vetus (Kellogg)

FIGS. 3, 3a—Incomplete left ramus with P3-M1; No. 1962. Fig. 3, occlusal view, $\times 2\frac{1}{4}$; fig. 3a, lateral view, $\times 1\frac{1}{2}$. Middle Pliocene, Rome, Oregon.

Hypolagus near *limnetus* Gazin

FIG. 4—Incomplete left ramus with P3-M2; No. 1973; $\times 2\frac{1}{4}$; occlusal view. Middle Pliocene, Kern River Beds, California.

FIG. 5—Right ramus with P3-M3; No. 1972; $\times 1\frac{1}{2}$; lateral view. Middle Pliocene, Kern River Beds, California.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale.

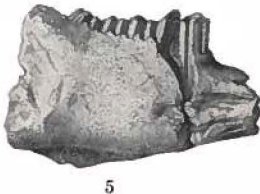
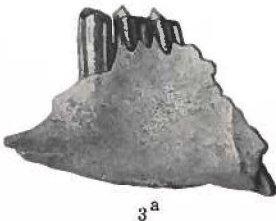
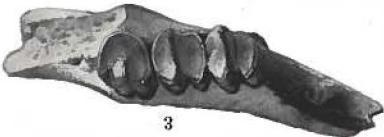
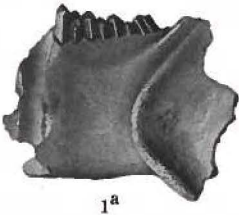
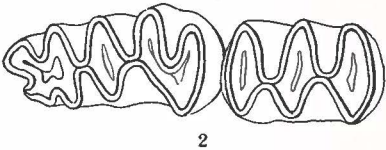


PLATE 3

Citellus? sp.

FIGS. 1, 1a—Right ramus with $P1-M2$; No. 1965; $\times 3$. Fig. 1, occlusal view; fig. 1a, lateral view.

Peromyscus pliogenicus n. sp.

FIGS. 2, 2a—Incomplete right ramus with $M1-M2$, type specimen; No. 1966. Fig. 2, occlusal view (reversed), $\times 6\%$; fig. 2a, lateral view, $\times 4\frac{1}{2}\%$.

FIG. 3—Fragment of right maxillary with $M1$ and incomplete $M2$ (reversed), paratype specimen; No. 1968; $\times 6\%$.

FIG. 4—Left ramus with $M1-M2$ (reversed), paratype specimen; No. 1967; $\times 6\%$.

Hypolagus near *limnetus* Gazin

FIG. 5—Incomplete maxillæ with right $P2-M2$ and left $P3-M2$; No. 1969; $\times 1\frac{1}{2}\%$.

FIG. 6—Fragmentary left maxillary with $P2-M2$; No. 1970; $\times 2\frac{1}{4}\%$.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale. Middle Pliocene, Kern River Beds, California.



1



2



1a



2a



3



4



5



6